A NEW SPECIES OF *ACHNATHERUM* (*ORYZOPSIS*) FROM OREGON

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ABSTRACT

A new species of *Achnatherum, A. wallowaensis* Maze and K. A. Robson of central and northeastern Oregon is closely related to *A. hendersonii* (Vasey) Barkworth (=*Oryzopsis hendersonii*) of central Washington and Oregon but differs from this species primarily in its lax inflorescence with drooping spikelets, *A. hendersonii* having stiff inflorescences with erect spikelets. Other differences in vegetative and reproductive features occur between these two taxa with *A. wallowaensis* tending to have longer, but thinner, parts. The two species show different relationships among their descriptive variables and are separated by a principal components analysis. Like its close relative, *A. wallowaensis* occupies small scattered areas of shallow, rocky soils that support a vegetation of small, distantly spaced plants.

Henderson's rice grass, *Achnatherum* (*Oryzopsis*) *hendersonii* (Vasey) Barkworth (nomenclature follows Barkworth [1993]) is a small bunch grass that grows in rocky shallow soils in Washington and Oregon. Until recently its distribution was known only from central Washington and central Oregon (Hitchcock et al. 1969) but, through the efforts of botanists employed by the United States Forest Service and the Nature Conservancy in Oregon, many more instances of its occurrence have been discovered (Vrilakas 1990). The greatest number of new findings of this species have been made in the Wallowa Mountains of northeastern Oregon, with some populations also discovered in the Ochoco Mountains of central Oregon and the grasslands of southern Wasco County in Oregon.

As part of a study into the nature of variation in grass species of restricted distribution, we visited the Wallowa Mountains in the summer of 1991 and noted that plants called *A. hendersonii* growing there differed from those of central Washington in their lax inflorescences and drooping spikelets. The plants of central Washington have stiff inflorescences with erect spikelets, features noted both in recent descriptions (Hitchcock et al. 1969) as well as in the original

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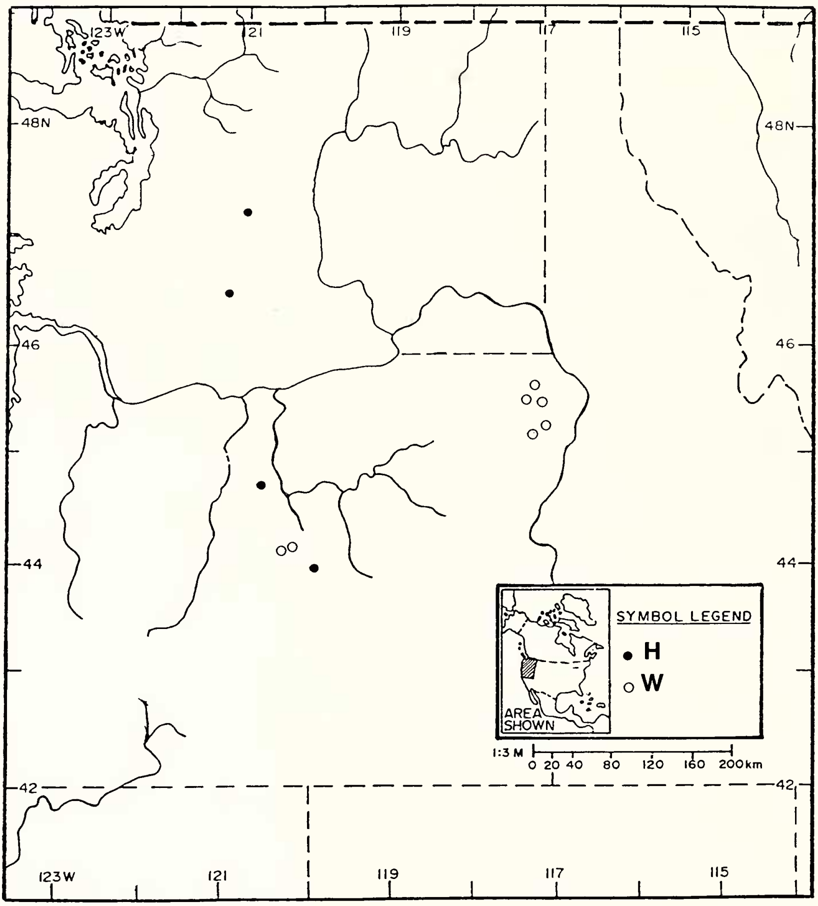

FIG. 1. Distribution of *A. hendersonii* (solid circles) and lax inflorescence forms (open circles).

species description (Vasey 1894). This stimulated a field trip in the summer of 1993 to determine the distribution and abundance of the plants bearing lax inflorescences. We wanted to know if the plants with lax inflorescences had a unique distribution and if that feature had a distinctive relationship with other morphological attributes, suggesting two unique taxa, perhaps even species.

MATERIALS AND METHODS

Plants from throughout the range of *A. hendersonii* (*sensu lato*) were collected in June of 1993. The collection sites are shown in Figure 1. We collected all specimens except those from north-central

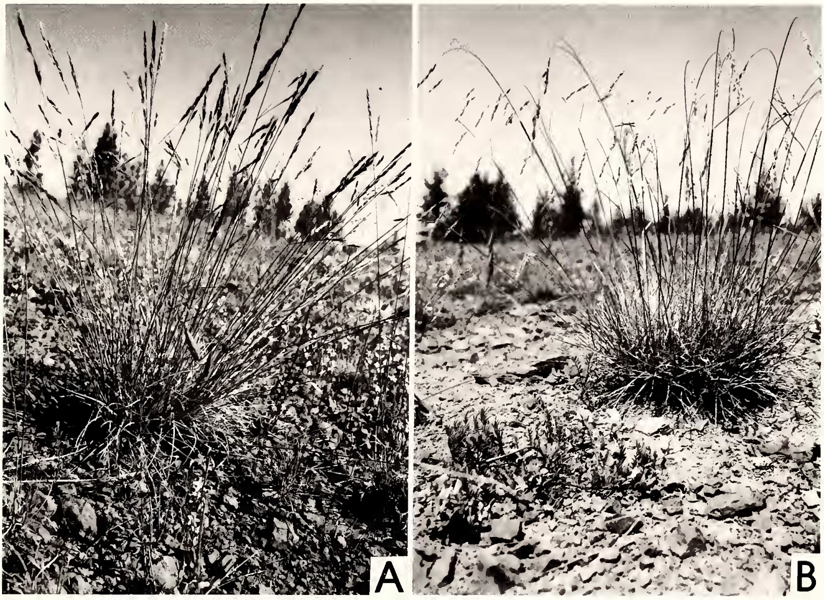

FIG. 2. Photographs of *A. hendersonii* (A) and lax inflorescence form (B) both from the Ochoco Mountains.

Oregon, which were collected by Jonathan Soll of the Nature Conservancy. We also borrowed the type of *A. hendersonii,* collected on Clemans Mt. in south-central Washington, to include in our comparisons.

Examples of both forms of what has been called *Achnatherum hendersonii* are shown in Figure 2. The plants from Washington, including the type, specimens from north-central Oregon, and some from central Oregon have stiff inflorescences with erect spikelets. Those from northeastern Oregon and some from central Oregon have lax inflorescences with drooping spikelets. These different forms do not share a common distribution (Fig. 1).

In order to quantify the variation in these grasses and to discover if the differences between them extended beyond general inflorescence features, we performed a principal components analysis (PCA) of a large set of spikelet, inflorescence, and flag leaf characters. The variables were sheath, blade, and ligule length for the flag leaf; length and width of the two glumes and the floret, and the length of the thickened portion of the lemma apex on the adaxial side of the lemma; inflorescence type (erect or drooping), the length of the lowest inflorescence branch, the total length of the inflorescence from the lowest node to the tip of the topmost spikelet, the thickness of the inflorescence axis at its midpoint, and the thickness of the lowest inflorescence branch at its midpoint. The spikelet measurements were taken from the terminal spikelet of the lowermost inflorescence branch. All variables except inflorescence type were measured, inflorescence type was coded as either lax (1) or stiff (2). This coding was done when the plants were collected since lax inflorescences often straightened during drying in a press. We are aware of the undesirability of using coded variables in a PCA. However, the difficulty in measuring degree of laxness as other than a binary variable in the field, and the impossibility of doing so on herbarium specimens after they dried and straightened, left us little choice. And the character, to us, apppears real, remaining constant within populations.

The PCA was done in two steps. First, all variables were subjected to PCA of a correlation matrix. That PCA was used to eliminate variables that were redundant (those that had very similar loadings over all eigenvectors) or those that were most weakly related to the major trends of variation in the pooled data. The latter were assessed as described in Maze et al. (1992), i.e., prorating of eigenvector values based on the percent variation for which the various axes account, and then summing over all eigenvectors. This initial comparison and adjustment of variables was made without assuming that two taxa exist. If they do then a multivariate analysis of those variables whose importance is determined independently should still reveal their existence.

As the end result of these manipulations, the variables subjected to a second PCA were INFLTYPE (inflorescence form, lax or erect), SHEATH (length of the sheath of the flag leaf), BLADE (length of blade of flag leaf), G1L (length of the first glume), FL (length of floret, including the callus), FW (width of floret), AXISTHCK (thickness of the midportion of the inflorescence axis), BRNLN (length of the lowermost inflorescence branch), and INFLN (inflorescence length). The plants used in the analysis were those collected in 1993 and the type specimen of *A. hendersonii.* Means and standard deviations for plants with different inflorescence types were calculated for the variables described above.

Another comparison based on the recognition of two species was made. The variable interrelations within each of the putative species were assessed through determinants of correlation matrices and the angle between the first principal axes from the correlation matrices and a vector of isometry. The determinant is a statistic, a generalized variance, that describes the absolute values of the off-diagonal elements in a matrix. As the elements approach 0.0, the determinant of a correlation matrix approaches 1.0, as those off-diagonals come to approximate 1.0, the determinant of a correlation matrix becomes closer to 0.0. A vector of isometry is a theoretical vector derived from a matrix in which all the off-diagonal elements are identical. As such, a vector of isometry offers a means to describe the off-

TABLE 1. COMPARISON OF VARIABLES MOST CLOSELY RELATED TO MAJOR AXES OF VARIATION BETWEEN LAX INFLORESCENCE FORM AND *A. HENDERSONII*, Mean Above, Standard Deviation Below. SHEATH, length of the sheath of the flag leaf in cm; BLADE, length of blade of flag leaf in cm; INFLN, inflorescence length in cm; AXISTHCK, thickness of the midportion of the inflorescence axis in mm; BRLN, length of the lowermost inflorescence branch in mm; G1L, length of the first glume in mm; FL, length of floret in mm; FW, width of floret in mm; *, groups significantly different at P < 0.05.

	A. hendersonii	Lax inflorescence form
Variables		
SHEATH*	6.250	8.434
	1.106	1.474
BLADE	3.113	3.080
	0.816	0.930
INFLN*	8.267	10.623
	2.069	2.033
AXISTHCK*	1.123	0.803
	0.239	0.113
BRLN*	3.368	4.785
	1.112	1.255
G1L*	4.728	5.186
	0.657	0.642
FL*	4.530	4.216
	0.542	0.533
FW	1.388	1.351
	0.232	0.181

diagonal elements of a correlation matrix derived from measured variables through calculating the angle between a vector of isometry and a first principal axis derived from measured variables. As that angle increases, to a maximum of 90 degrees, the off-diagonal elements in a correlation matrix derived from measurements become increasingly different. These statistics can also be viewed as estimators of among-variable variation (Rapson and Maze 1984). As either determinants or angles with a vector of isometry increase, the among-variable variation increases.

RESULTS

Table 1 presents the means and standard deviations for those variables, averaged for each putative taxon, that were subjected to PCA. Inflorescence type is not included in this table as it was a binary variable. Not only are there differences in inflorescence form but also in the lengths of sheaths of the flag leaf, inflorescence, lowest inflorescence branch, first glume and floret and the thickness of the axis of the inflorescence. Generally speaking, the variables for the lax inflorescence form have the higher values, aside from floret length and thickness of the inflorescence axis.

Table 2 presents the results of the PCA and the graphic results of

TABLE 2. RESULTS OF PCA. INFLTYPE, inflorescence form; SHEATH, length of the sheath of the flat leaf; BLADE, length of blade of flag leaf; G1L, length of the first glume; FL, length of floret; FW, width of floret; AXISTHCK, thickness of the mid-portion of the inflorescence axis; BRLN, length of the lowermost inflorescence branch; INFLN, inflorescence length.

Eigenvalues	3.339	1.951	1.621
Percent variance accounted for	37.097	21.679	18.008
Eigenvectors			
SHEATH	0.897	0.038	0.000
BLADE	0.452	0.355	0.559
INFLTYPE	−0.732	0.439	0.411
AXISTHCK	−0.365	0.304	0.793
INFLN	0.835	−0.114	0.432
BRLN	0.790	−0.156	0.297
G1L	0.567	0.605	−0.392
FL	0.045	0.890	−0.172
FW	0.125	0.585	−0.228

this PCA are presented in Figure 3; the two grasses are separated from each other to some degree with *A. hendersonii* occupying the left hand portion of the ordination and the lax inflorescence forms grouping to the right.

The lax inflorescence form most similar to *A. hendersonii* on the first axis, those individuals designated by solid squares in Figure 3, came from an area with a very thin soil that was grazed by cattle. Whether it is the edaphic factors, the impact of cattle, or both, that are related to the form of the plants, they tend to be smaller than others with lax inflorescences as shown in Table 3, a comparison of the measured variables and PCA axis scores among *A. hendersonii,* the lax inflorescence forms, and such designated by the solid squares in Figure 3. The grazed specimens of the lax inflorescence form are as similar to *A. hendersonii* as they are to plants with similar inflorescences on the major axis of variation, the first principal axis.

Interestingly, the *A. hendersonii* that tend to be most similar to the lax inflorescence form (there is, in fact, some overlap among these plants) are the most distantly removed geographically, coming from central Washington. The plants of *A. hendersonii* geographically closest to the lax inflorescence form, those from central and northern Oregon, are the most distantly removed from them in the scatter plot in Figure 3. The specimen designated T is the type specimen of *A. hendersonii*; it is nested within the samples of *A. hendersonii.*

Figure 3 depicts the relationship among individual plants, an assessment of among plant variation. Estimators of among-variable relationships, determinants and angles with a vector of isometry, indicate they are different for the plants with the different inflores-

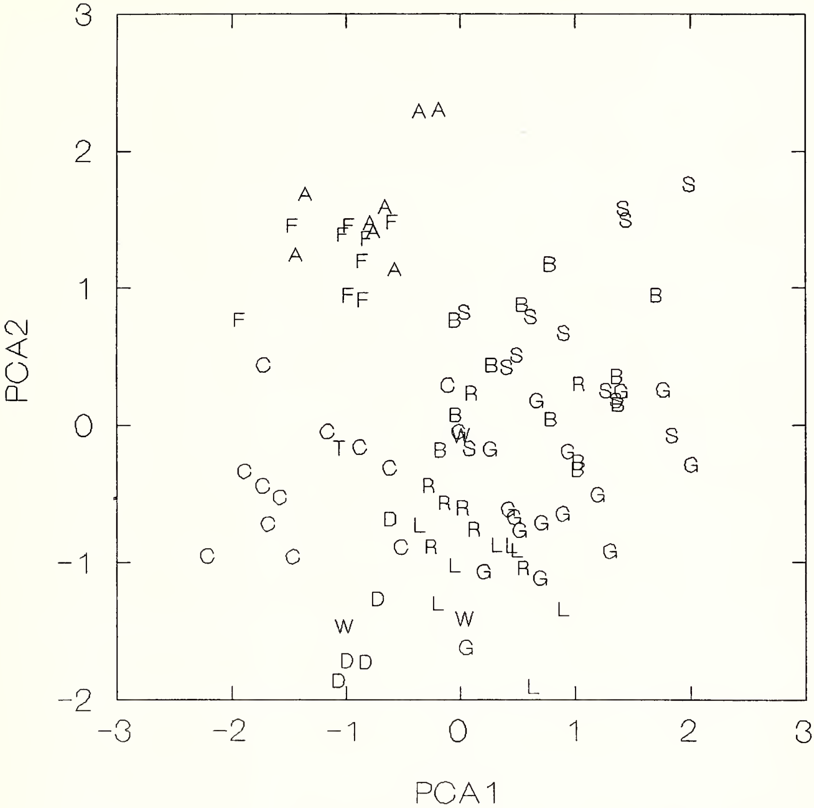

FIG. 3. PCA of length of the sheath of the flag leaf, length of blade of flag leaf, inflorescence type, inflorescence length, thickness of the midportion of the inflorescence axis, length of the first glume, length of floret, width of floret. Open stars, *A. hendersonii*; open squares, the lax inflorescence form; closed squares, the lax inflorescence form that has been grazed; PCA 1, first principal axis, 31.634% of the variation in the data; PCA 2, second principal axis, 25.921% of the variation in the data.

cence forms. *Achnatherum hendersonii* has a determinant of 0.020 and an angle between the first principal axis and a vector of isometry of 86.87 as compared to 0.003 and 15.67 respectively for the plants with lax inflorescences.

DISCUSSION

The plants of unlike inflorescence form also differ in other morphological features. As well, the two forms have unique geographic distributions and divergent patterns of among-variable relationships. The type of *A. hendersonii* has a stiff inflorescence with erect spike-

TABLE 3. COMPARISON OF *A. HENDERSONII* (AH), the Lax Inflorescence Form (AW), and the Lax Inflorescence Form that has been Grazed (AWD). Mean above, standard deviation below. SHEATH, length of the sheath of the flag leaf in cm; BLADE, length of blade of flag leaf in cm; INFLN, inflorescence length in cm; BRLN, length of lowermost inflorescence branch in cm; AXISTHCK, thickness of the midportion of the inflorescence axis in mm; G1L, length of the first glume in mm; FL, length of floret in mm; FW, width of floret in mm; PCA1–PCA3, scores on first three PCA axes; underlined means identify those that are statistically significant ($P < 0.05$).

	AH	AW	AWD
Variables			
SHEATH	6.250	<u>8.603</u>	6.400
	1.106	1.397	0.616
BLADE	3.113	3.180	<u>1.880</u>
	0.816	0.892	0.396
INFLN	8.267	<u>10.850</u>	7.900
	2.039	1.940	0.768
AXISTHCK	<u>1.124</u>	0.803	0.812
	0.239	0.115	0.099
BRLN	3.368	<u>4.917</u>	3.200
	1.112	1.213	0.292
G1L	4.735	<u>5.267</u>	4.303
	0.658	0.599	0.524
FL	4.537	4.267	<u>3.681</u>
	0.543	0.527	0.276
FW	1.391	1.363	1.218
	0.232	0.179	0.171
PCA1	−1.072	<u>0.606</u>	−0.841
	0.542	0.655	0.187
PCA2	<u>0.643</u>	<u>−0.201</u>	<u>−1.450</u>
	0.992	0.815	0.484
PCA3	<u>0.602</u>	−0.239	−0.737
	1.239	0.727	0.565

lets, a point noted in its species description. This suggests that the lax inflorescence form represents a new taxon. There is the question, however, of the level at which that new taxon should be recognized. Its closest relative is obviously *A. hendersonii*; both taxa share mature florets of comparable size that are shiny, brown to black at maturity, glabrous and indurate. As well, both have a thickened portion at the adaxial side of the lemma apex that extends above the base of the awn, and the palea is subequal to the lemma. The separation between *A. hendersonii* and the lax inflorescence form in the scatter plot (Figure 3) is not great; its magnitude is similar to that seen for the two subspecies of *Hesperostipa (Stipa) comata* (Trinius and Ruprecht) Barkworth, ssp. *comata* and ssp. *intermedia* (Scribner and Tweedy) Barkworth (Barkworth 1978).

In spite of strong similarities to *A. hendersonii* and a degree of separation in an ordination similar to that of subspecies of another species in the Stipeae, we decided to recognize this new taxon at the specific level as *Achnatherum wallowaensis* Maze and K. A. Robson. There are five reasons for this decision. First, the two taxa are consistently separated by one very distinct morphological feature: drooping inflorescences for *A. wallowaensis* and erect ones for *A. hendersonii.* There are no known intermediates. Second, these two taxa differ in other features such as length of sheaths, inflorescences, longest branch of the inflorescence, first glume, and floret and thickness of the inflorescence axis. Third the two taxa, *A. wallowaensis* and *A. hendersonii,* do not occur sympatrically although they are within 20 kilometers of each other in the Ochoco Mountains in central Oregon. Fourth, the individuals of *A. hendersonii* most similar to *A. wallowaensis* are the most distant geographically. Fifth, the among variable relationships are different for the two species. The species description appears below.

A final observation we would make is that seedlings appear to be extremely rare in many of the *A. hendersonii* populations, while seedlings were numerous for at least one of the populations of *A. wallowaensis* from northeastern Oregon. Both of these species are rare and reproduction needs further study.

Achnatherum wallowaensis Maze and K. A. Robson sp. nov.—TYPE: USA, Oregon: Wallowa Co., Wallowa-Whitman National Forest, ca. 34 km N of Enterprise, near Boner Gulch along Forest Service Road 46, 1481 m, 45°43′41.16″N × 117°8′10.32″W (SW ¼ of SE ¼, section 24, T 3 N, R 45 E). *J. and E. Maze, K. A. Robson, T. Henn 1007* 26 June 1993. (holotype, US; isotypes, UTC, UBC, WTU, OCS, COLO, NMC, DAV, UC, ID).

Perenis gramen sine rhizoma, (1)1.5–4(4.5) dm altus; vegetativus lamina erectus et valde involutus; inflorescentia (6.3)8.1–12.6(14.8) cm longus, laxus cum spicula cernuus; spicula cum unus anthracinus ad brunneus induratus flosculus (3.0)3.5–5.0(5.5) cm longus, aequalis gluma; arista deciduus 8–10(11) mm longus; palea subaequalis lemma.

Non-rhizomatous perennial; culms solid to hollow, (1)1.5–4(4.5) dm tall; sheaths glabrous to puberulent; blades strongly involute, erect to sometimes reflexed in the flag leaf, glabrous ventrally, pubescent dorsally; panicle (6.3)8.6–12.6(14.8) cm long, broadly spreading with lax branches and drooping spikelets on curved pedicels; glumes obtuse to acute, first (3.5)4.5–6.0(7.0) mm long, second (3.0)4.0–4.5(6.5) mm long; floret (3.0)3.5–5.0(5.5) mm long, 1.0–1.5 mm wide, apex of dorsal side of lemma thickened, maturing black to dark brown; awn 8–10(11) mm long, readily deciduous; palea subequal to the lemma; anthers 1 mm long or less, ventral lodicule reduced.

Paratypes. USA, Oregon: Crook Co., ca. 30 km NE of Prineville, Ochoco National Forest near U. S. Forest Service Road 2730, Bull Mountain, 1481 m, 44°31′47.28″ N × 120°36′56.52″W (border between SE ¼, section 7 and NE ¼, section 18, T 12 S, R 18 E), plants growing in shallow rocky soil with *Mimulus nanus, Astragalus whitneyi, Clarkia pulchella, Phlox hoodii, Eriogonum compositum* var. *compositum, Poa sandbergii, Arenaria rubella, Danthonia intermedia, Erigeron chrysopsidis* var. *chrysopsidis, Lomatium macrocarpum, Blepharipappus scaber, Sedum stenopetalum* (Plant names here and elsewhere follow Hitchcock and Cronquist 1973), *J. and E. Maze 1001,* 22 June 1993 (US, UTC, UBC, WTU, OCS, COLO, NMC, DAV); Ochoco National Forest, ca. 30 km NE of Prineville, near U.S. Forest Service road 2730, ca. .8 km SE Skookum Rock, 1353 m; 44°33′15.12″N × 120°34′31.44″W (middle, section 9, T 12 S, R 18 E), plants growing in shallow rocky soil with *Mimulus nanus, Astragalus whitneyi, Clarkia pulchella, Phlox hoodii, Eriogonum compositum* var. *compositum, Poa sandbergii, Arenaria rubella, Danthonia intermedia, Erigeron chrysopsidis* var. *chrysopsidis, Lomatium macrocarpum, Blepharipappus scaber, Sedum stenopetalum; J. and E. Maze 1002,* 22 June 1993 (US, UTC, UBC, WTU, OCS, COLO, NMC, DAV, UC, ID); Wallowa Co., ca. 15 km E of Joseph, near Cat's Back along Wallowa Co. Road 673, 7.8 km from Oregon State Highway 350, 1584 m, 45°20′45.96″N × 117°00′50.76″W (SE ¼ of NW ¼, section 36, T 2 S, R 46 E), plants growing in shallow rocky soil with *Bromus tectorum, Sitanion jubatum, Mimulus nanus, Lomatium cous, Haplopappus lanuginosus* var. *lanuginosus, Poa sandbergii, Scutellaria antirrhinoides, Alyssum alyssoides, Penstemon elegantulus, Eriogonum douglasii, Tragopogon dubius, Polygonum minimum, J. and E. Maze, K. A. Robson, T. Henn, M. Stein 1004,* 25 June 1993 (US, UTC); ca. 18 km ENE of Joseph, 19.7 km from Oregon State Highway 350 along Forest Service Road 900, Clear Lake Ridge, 1499 m, 44°25′10.56″N × 116°57′11.16″W (center, section 4, T 2 S, R 47 E), plants growing in shallow rocky soil with *Bromus tectorum, Alyssum alyssoides, Penstemon elegantulus, Eriogonum strictum* var. *strictum, Allium tolmei, Tragopogon dubius, Polygonum minimum; P. majus, Trifolium macrocephalum, Sedum stenopetalum, Lomatium cous, Poa sandbergii, Arabis* sp., *J. and E. Maze, K. A. Robson, T. Henn, M. Stein 1005,* 25 June 1993 (US, UTC, UBC, WTU, OCS, COLO, NMC); Wallowa-Whitman National Forest, ca. 24 km N of Enterprise, near Roberts Butte, along Forest Service Road 4605 near its junction with Forest Service Road 46, 1097 m, 45.°38′23.64″N × 117°13′3.36″W (middle southern boundary, section 20, T 2 N, R 45 E), plants growing in shallow rocky soil with *Bromus japonicus, Blepharipappus scaber, Mimulus nanus, Eriogonum strictum, Scoutellaria antirrhinoides, Lomatium macrocarpum, L. dissectum, L.*

triternatum, L. ambiguum, L. sp., *Sedum stenopetalam, Penstemon deustus, Epilobium* sp., *Clarkia pulchella, Allium tolmei, Poa scabrella, P. sandbergii, J. and E. Maze, K. A. Robson, T. Henn, 1006,* 26 June 1993 (US, UTC, UBC, WTU, OCS); Wallowa-Whitman National Forest, ca. 37 km N of Enterprise, on ridge just S East Fork of Sumac Creek, at end Forest Service Road 268 off of Forest Service Road 46, 1292 m, 45°45′27″N× 117°8′10.32″W (NE ¼ of NW ¼, section 12, T 3 N, R 45 E), plants growing in shallow rocky soil in site badly disturbed by cattle with *Poa sandbergi, Agropyron spicatum, Sedum stenopetalam, Chrysothamnus nauseosus, Polygonum majus, Phlox hoodii, J. and E. Maze, K. A. Robson, T. Henn, 1008* 26 June 1993. (US, UTC, UBC).

Distribution. Shallow rocky soils in scattered localities at 1000–1600 m in the Wallowa Mountains of northeastern Oregon and Ochoco Mountains of central Oregon.

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